2014

The Inactivation of the Gene NF2 and Its Protein Product Merlin as a Mechanism of Malignant Mesothelioma

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Advanced Cell and Molecular Biology
4/1/14

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Malignant mesothelioma is an extremely aggressive form of cancer that affects mesothelial cells. These cells act to form a slippery and protective layer of cells that line the serous cavities and internal organs of the body. Malignant mesothelioma most often develops in the pleural space, but also arises in the peritoneum, pericardium, tunica vaginalis testis, and ovarian epithelium (Vinícius and Isoldi, 2013). Evidence has shown a strong relationship between asbestos exposure and malignant mesothelioma, and this is the most widely known disease vector of malignant mesothelioma. Asbestos is a family of carcinogenic silicate fibers that are able to infiltrate and damage the pleural space of the lungs and is tightly correlated with malignant mesothelioma. However, exposure to erionite and simian virus 40 (SV40), as well as genetic predisposition, have also been associated with malignant mesothelioma (Vinícius et al., 2014). Despite these alternate agents, the leading cause of the disease remains asbestos exposure. Studies have shown that 80% of individuals diagnosed with malignant mesothelioma had previous asbestos exposure. Asbestos is a common material used in many commercial products because it is cost effective and has useful properties in many industries. The result is that despite it deadly affects, asbestos has not been banned by most countries including the U.S. and is still in wide use today. In fact, in 2003 over 2 million tons were mined and used in products worldwide (Vinícius and Isoldi, 2013).

Malignant mesothelioma displays an unusually long latency period, often up to 40 years after exposure before being diagnosed. It is believed that during this time mutations arise in key regulatory genes. This results in over 60% of malignant mesothelioma patients being diagnosed in the fifth and seventh decade of their life. Males are at a much higher risk for developing the disease, most likely because of occupational exposure (Vinícius and Isoldi, 2013). The disease is often diagnosed in the late stages and acts quickly. Prognosis is grim, and treatments are largely ineffective and have changed little over time. Median survival after diagnosis is just 11 months. Because of both continued exposure as well as the usually long latency period, the disease will remain a problem for the foreseeable future. It is expected that 70,000 new cases of malignant mesothelioma will arise over the next 20 years in the U.S. alone (Vinícius et al., 2014). While it may be difficult to prevent all asbestos exposure, studying and understanding the cellular mechanisms of this aggressive disease will aid in developing new treatments to better combat it and help thousands of patients across the world.

The mechanism by which asbestos causes malignant mesothelioma is still not fully understood, but is thought to be multifaceted. One proposed map of the pathways involved is shown in figure 1. It is known that airborne particles of asbestos become trapped inside the lungs triggering an inflammatory

response of pro-inflammatory cytokines that results in the activation of promoters of antiapoptotic genes called oncogenes (Vinícius and Isoldi, 2013). The specific pathways and implicated genes and proteins of the disease are multifaceted, not fully understood, and numerous. However, key discoveries have given some insight, and several possible pathways have come to light.

Generally, it has been shown that malignant mesothelioma often exhibits loss of chromosomes 1, 3, 4, 6, 9, 13, 14 and 22. One of the most common changes in diseased cells is the homozygous deletion of *p14ARF* and of *p16INK4a* genes. Both of which are involved in cell cycle regulation by regulating the G1/S checkpoint of the cell cycle. p16INK4A is a INK4 protein and has been identified as a tumor suppressor in many cancers. p14ARF protein inhibits the mdm2/p53/p21 pathway and also acts as a tumor suppressor. In contrast to this finding, and unlike many other cancers, the protein p53 encoded by *TP53* has been found to have a fairly low mutation rate in the disease. This gene plays an important role in the cells response to DNA mutations. Although it has not been ruled out in malignant mesothelioma, it is not fully understood. Also, the PI3K/AKT/mTOR pathway has shown to be activated in the disease and is responsible for cell proliferation, survival, and metastasis in most cancers. In relation to this pathway, the gene *PTEN* has also been implicated as perhaps a pathway regulator and being altered in the disease. However, this is a new development and is ongoing. One pathway of increasing interest is the tumor suppressor Neurofibromatosis type II (*NF2*). Although not an initial focus of research, several recent studies have shown *NF2* inactivation is a frequent event in the disease with rates ranging from 20% to 60%. *NF2* is associated with the suppression of several mitogenic signaling pathways. This *NF2* pathway will be the basis of investigation for this paper. Lack of expression has been previously associated with brain tumors, and other cancers. *NF2* is located on chromosome 22q12, and codes for a 595 amino acid protein called Merlin (Moesin-ezrin-radixin-like protein). The first groups to look at *NF2's* implication in malignant mesothelioma demonstrated that it was mutated in approximately 40–50% of cases, leading to the conclusion that its suppression was important in the tumorigenesis of the disease. Recent studies have strengthened this data. They show that 38% of pleural malignant mesothelioma samples displayed *NF2* mutation, and 29.4% displayed deletions. This is in contrast to non- malignant mesothelioma lung cancer where no *NF2* mutation was discovered. Other studies have found miRNA expression targeting *NF2* in the disease (Vinícius et al., 2014). Although the cellular mechanism of *NF2* tumor suppression is not fully understood, the protein product of the gene is structurally related to the Ezrin–Radixin–Moesin (ERM) family of proteins. These proteins are known to act as linkers between membrane and the cytoskeleton. Similar to the ERM proteins, merlin has an amino-terminal protein 4.1 family domain (FERM), as well as a long C-terminal alpha helical region. Also, the localization of merlin at areas of membrane remodeling point to functions related to the invasive properties of malignant cells as well as cell adhesion,

communication, and motility (Poulikakos et al., 2006). The implications of *NF2* suppression on downstream signaling pathways that may be disrupted as a result of this inactivation are not entirely understood. However, recent work has focused on *NF2* acting as a regulator to other pathways implicated in malignant mesothelioma (Vinícius et al., 2014). Such pathways include the genes, *P53, YAP1*, and *PTEN*. This research is in its beginning stages, but has offered exciting preliminary information that *NF2* could act primarily as a regulator of other oncogenes (Yokoyama et al., 2008).

One of the first steps in understanding *NF2's* regulation in malignant mesothelioma was to actually determine if the gene was altered in diseased tissues and to what extent. One group collected patient tissue samples from 44 malignant mesothelioma cases in order to better understand the relationship. Three asbestosis patients' and six normal pleura patients' tissues were also examined as a control. Tissue samples were cultured and analyzed in terms of the characteristics of *NF2*. The researchers accomplished this primarily by means of PCR and western blot analysis (Thurneysena et al., 2009). RNA was extracted from the cells using a standard RNA extraction kit. From this RNA, reverse transcription was performed on 400–500 ng RNA. Full length *NF2* cDNA was amplified using PCR and primers. Further PCR was performed on the full length *NF2* cDNA. Truncated *NF2* transcripts were found in 20.5% of malignant pleural mesothelioma samples. Knowing that some samples may not contain detectable changes in the size of the *NF2* transcript, and that point mutations could still be present and affect protein expression, the researchers decided to further investigate characteristics of *NF2's* protein product merlin in the samples. To do this, they performed western blots on the cell cultures and found that 43% of the malignant mesothelioma cultures showed an absence of merlin (Thurneysena et al., 2009).

With these simple experiments, researchers found that the product of the *NF2* gene merlin is either absent or inactive in a large percentage of cultures obtained from mesothelioma patients. The overall frequency of *NF2* alteration at either the mRNA or protein level was 43%. These two findings were significant because they established a high level of *NF2* alteration in malignant mesothelioma tissue samples and established a correlation between the two. Critics may point out that only 43% of samples had detectable alterations of merlin. However, this number is significant in a disease such as malignant mesothelioma where the pathways are multifaceted and not necessarily exclusive. Also, the researchers pointed out that merlin can be phosphorylated on Ser518, which causes functional inactivation. Therefore, they propose that further research will likely reveal that functional disruption of *NF2* signaling is present in all mesothelioma cells (Thurneysena et al., 2009).

A second research team took the experimentation on *NF2* to the next level by re-expressing the gene in malignant mesothelioma cells and observing the effects on the cells' tumor like properties.

Knowing that malignant mesothelioma is a highly invasive cancer and massive local spreading is common, they chose to compare local spreading (wound healing) in cells from two malignant mesothelioma cell lines (Meso17, Meso25) that either had non-functional *NF2* or had been restored to have functional *NF2*. An adenovirus construct that expresses NF2-518A and green fluorescent protein (GFP) transfect cells and restore *NF2*. The GFP ensured the re-introduction of active merlin into a high percentage of diseased cells after it was shown to be expressed in more than 95% of the cells. A control of *NF2*-deficient malignant mesothelioma cells infected with empty adenoviral vector was also performed. The assay was monitored by time-lapse videomicroscopy as cells were cultured and grown to confluency. After infection with the virus, a wound channel was made down the center of each well with a sterile pipette. Time-lapse images were captured at 10 minute intervals over a 24 hour period and temperature was controlled at 37° C. The surface area covered by the cells as well as velocity of cell spreading was then estimated. They found that re-expression of merlin resulted in a marked decrease in the motility of the cells into the wound area of both Meso17 and Meso25 cells compared with the control infected cells. Although these cells were still technically a malignant mesothelioma cell line, their tumor like spreading properties showed a marked decrease. Specifically, cells expressing functional merlin covered about half of the empty surface area that was covered by the control cells that had non-functional merlin. It was also discovered that cells with re-expressed functional merlin consistently moved with less velocity than cells with no functional *NF2* or merlin. Data and images displaying this finding are shown in Figure 2 (Poulikakos et al. 2006).

Increased invasiveness and cell motility in vitro is known to correlate with greater malignant and invasive properties in vivo. Since both the area infiltrated and the velocity of movement were greater in cells that had non-functional *NF2* than cells where *NF2* was re-expressed, the experiment provides clear evidence that *NF2* and its protein product have a direct effect on the tumor-like properties of malignant mesothelioma. This suggests that merlin either performs independent functions of tumor suppression, or regulates a pathway that in turn imparts tumor suppression. This finding is significant in that it demonstrates a link between the presence of functional *NF2* and merlin and tumor like properties of malignant mesothelioma cells. This is an important implication of a model of malignant mesothelioma which involves the loss or suppression of *NF2* and merlin resulting in or at least contributing to the tumor like properties of diseased cells in malignant mesothelioma (Poulikakos et al. 2006).

Although evidence clearly demonstrates that *NF2* is modified in malignant mesothelioma, a third research team desired to uncover the actual mechanism in which *NF2* was inducing or contributing to malignant mesothelioma. The pathway is complex and not fully understood. However, they hypothesized that *NF2's* protein product, merlin, acted as a negative regulator of YAP1. YAP1is a protein encoded by

the YAP1 oncogene that has been shown to play a positive role in other malignant cancers. It acts as a transcriptional co-activator that up regulates genes that promote cell growth while also inhibiting apoptosis. The study first showed that downregulation of *YAP1* inhibited mesothelial cell proliferation, whereas upregulation *YAP1* induced mesothelial cell proliferation. This demonstrated a role of *YAP1* in malignant mesothelioma. To test the hypothesis that merlin acted as a negative effector of *YAP1*, researchers cotransfected both *YAP1* and *NF2* expression vectors into a malignant mesothelioma cell line with a prior deletion of the *NF2* gene. They then used immunoprecipitation to look at whether exogenous merlin has an effect on the phosphorylation status of *YAP1* by using an antibody against phosphorylated serine 127 of *YAP1*. This site was chosen because it is a critical phosphorylation site that has been shown to cause inactivation of *YAP1* as a transcription coactivator. The data collected from the experiment demonstrated that cotransfection with both *YAP1* and *NF2* expression vectors clearly induced the phosphorylation of *YAP1* at S 127 (Yokoyama et al., 2008) (figure 3 A and B).

The implications of this experiment were important because it was one of the first studies that aimed to uncover the cellular mechanism by which *NF2* acts to induce malignant mesothelioma. Other studies were important in establishing *NF2* as one of many genes that may be involved in the disease, but the true mechanism of action remained a mystery. Yokoyama et al. were among the first to propose a possible mechanism based on the results of this experiment. The data clearly indicates that Merlin-dependent phosphorylation inhibits the nuclear localization of *YAP1*, which might result in inactivation of *YAP1* transcriptional activity. Merlin does not act as a kinase and directly phosphorylate *Yap1*, but rather is thought to act by regulating the hippo signaling pathway which ultimately results in phosphorylation. This finding, when compounded with the knowledge that that activation of *YAP1* induced mesothelial cell proliferation, results in support for a mechanism of action for merlin. In this mechanism merlin acts as a pathway regulator that goes awry to induce or at least contribute to malignant mesothelioma. Specifically, the model proposes merlin causes phosphorylation of *YAP1* at the S 127 site which results in its inactivation. Since *YAP1* is a known malignant tumor activator, it reasons that merlin, which is lost with the alteration of *NF2*, acts to suppress the gene and inhibit malignant cell proliferation (or conversely permit malignant cell proliferation when absent). This was an important finding and sheds light on one possible mechanism in which *NF2* acts in malignant mesothelioma (Yokoyama et al., 2008).

The research presented has demonstrated a clear link between *NF2* alteration and malignant mesothelioma. The experiments have shown that *NF2* and merlin are inactivated or suppressed in a large percentage of malignant mesothelioma tissue cultures. Furthermore, it has been shown that re-expression of *NF2* in mesothelioma cell lines has resulted in a retraction of some tumor-like characteristics. Although the mechanism of action of *NF2* in relation to the gene remains complex, there is evidence that it at least

partially acts by regulating the expression of the *YAP1* gene product. These relatively recent findings bring optimism into potential new malignant mesothelioma treatments. Treatment options for the disease have remained relatively unchanged for many years, and the prognosis is grim for this very aggressive form of cancer. This combined with the continued use of asbestos results in a true need for new and effective treatments. *NF2* appears to be one of many genes involved with the disease that could offer a target for treatment of this deadly disease. If *NF2* suppression plays a role in causing the tumors, then it stands to reason that somehow turning the gene back on could result in an effective treatment. I believe that ample evidence has been uncovered showing *NF2's* role in the disease and that re-expression can result in reversal of tumor-like properties. With this, I believe that research should focus on methods of re-expressing the gene and the subsequent effects on malignant mesothelioma in an animal model. Perhaps gene therapy using transfection or even the development of a new drug could re-activate *NF2* and put its tumor fighting properties back to use. At a minimum, the data offers enough for further investigation of the pathway. Of further interest is research that was done at The University of Montana on the effect of *NF2* as a regulator of a separate pathway involving *P53* and *PTEN*. However, this research is young and needs to be explored further. What is clear at the present moment is that *NF2* and its protein product play an important role in mechanism of malignant mesothelioma and are deserving of further investigation as a potential therapeutic target.

Figures

Figure 1. A proposed pathway map of malignant mesothelioma. (Vinícius et al. 2014)

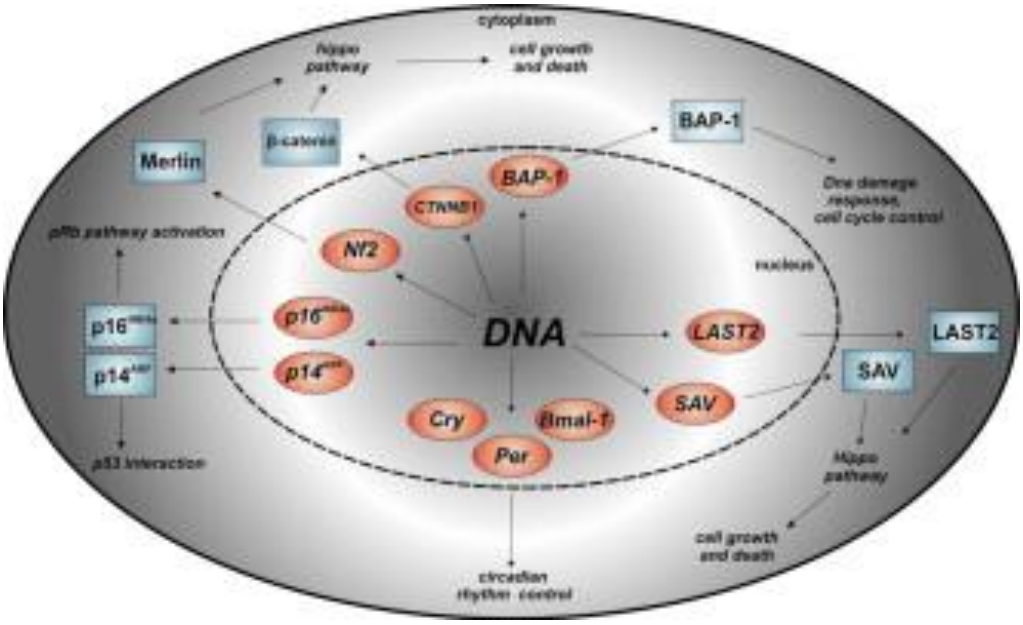


Figure 2. Re-expression of merlin on malignant mesothelioma cell motility. (Poulikakos et al. 2006)

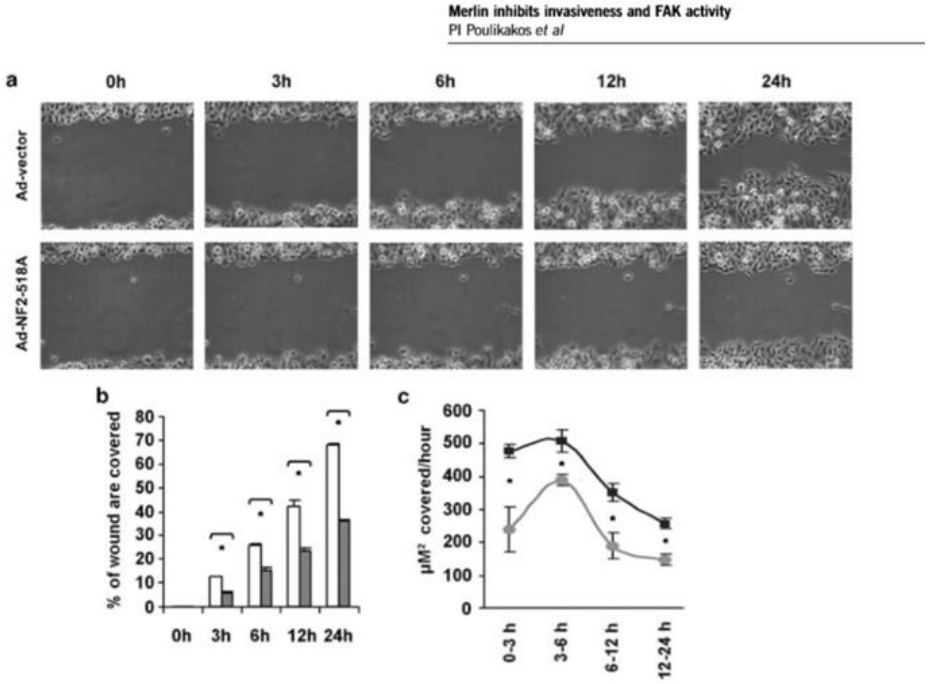
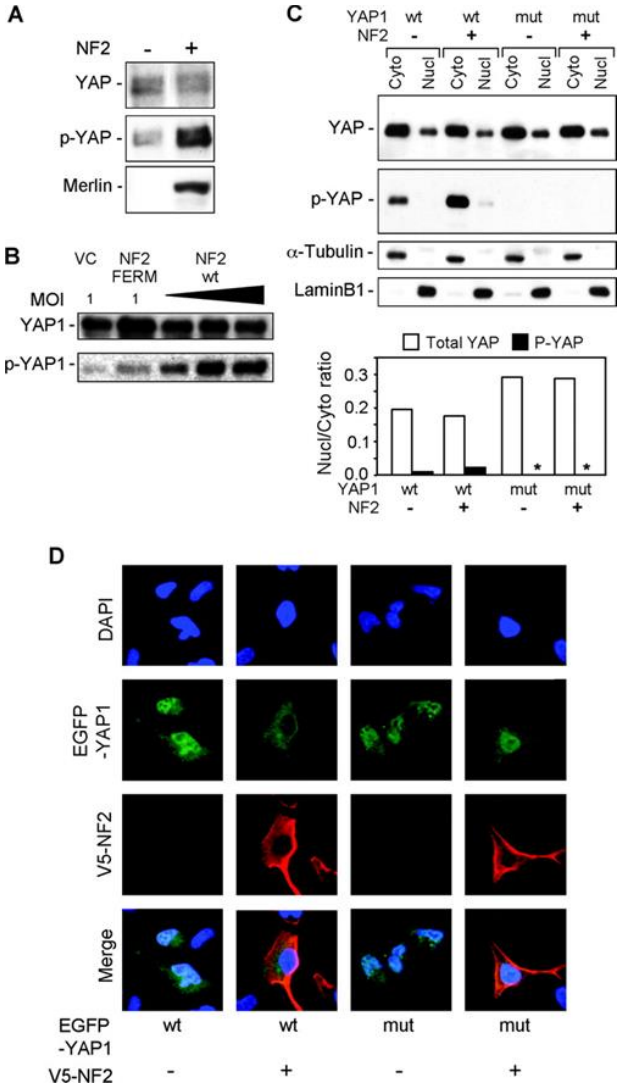


Figure 3. Functional Interaction between YAP1 and merlin. (Yokoyama et al. 2008)



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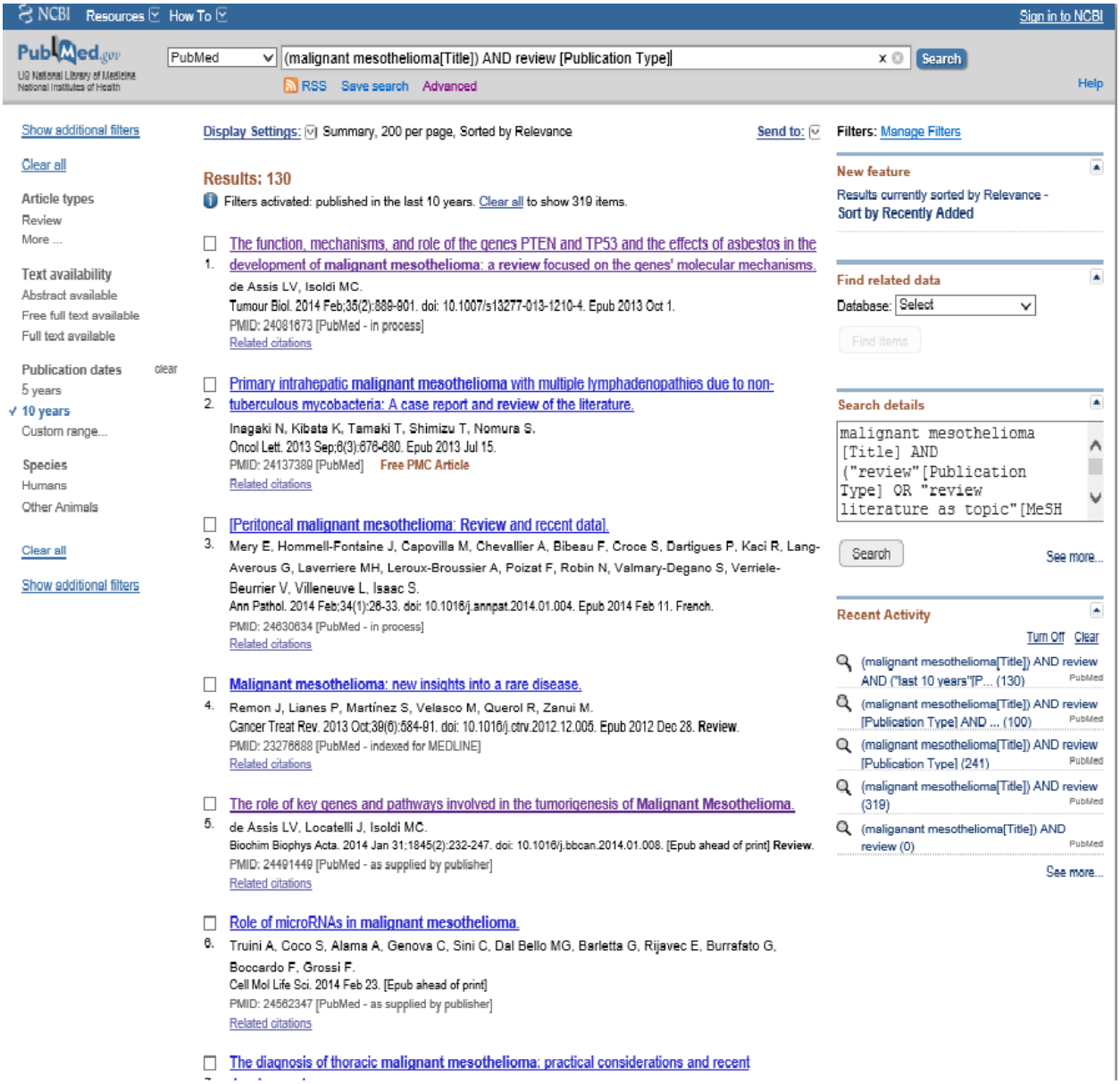

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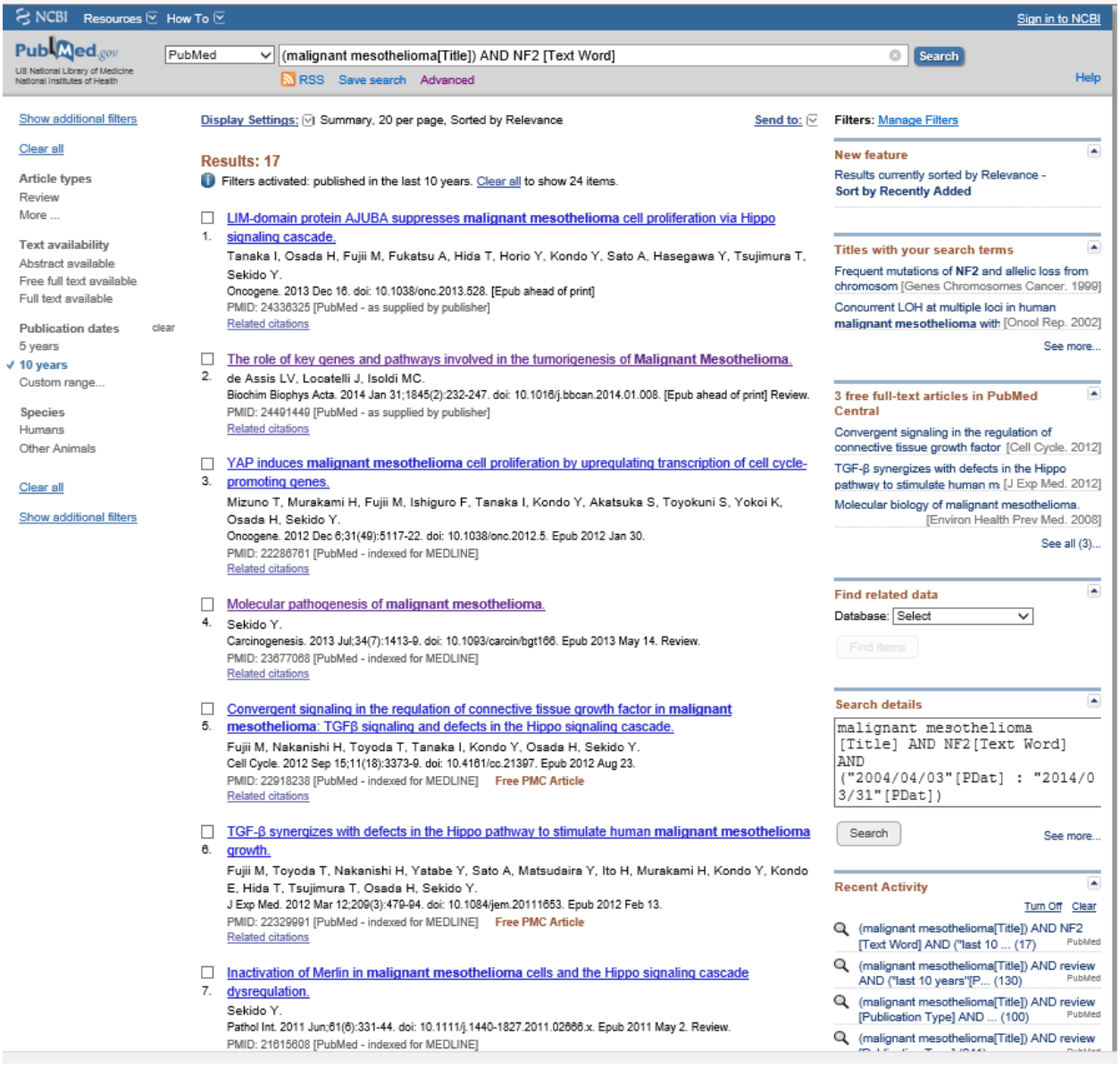
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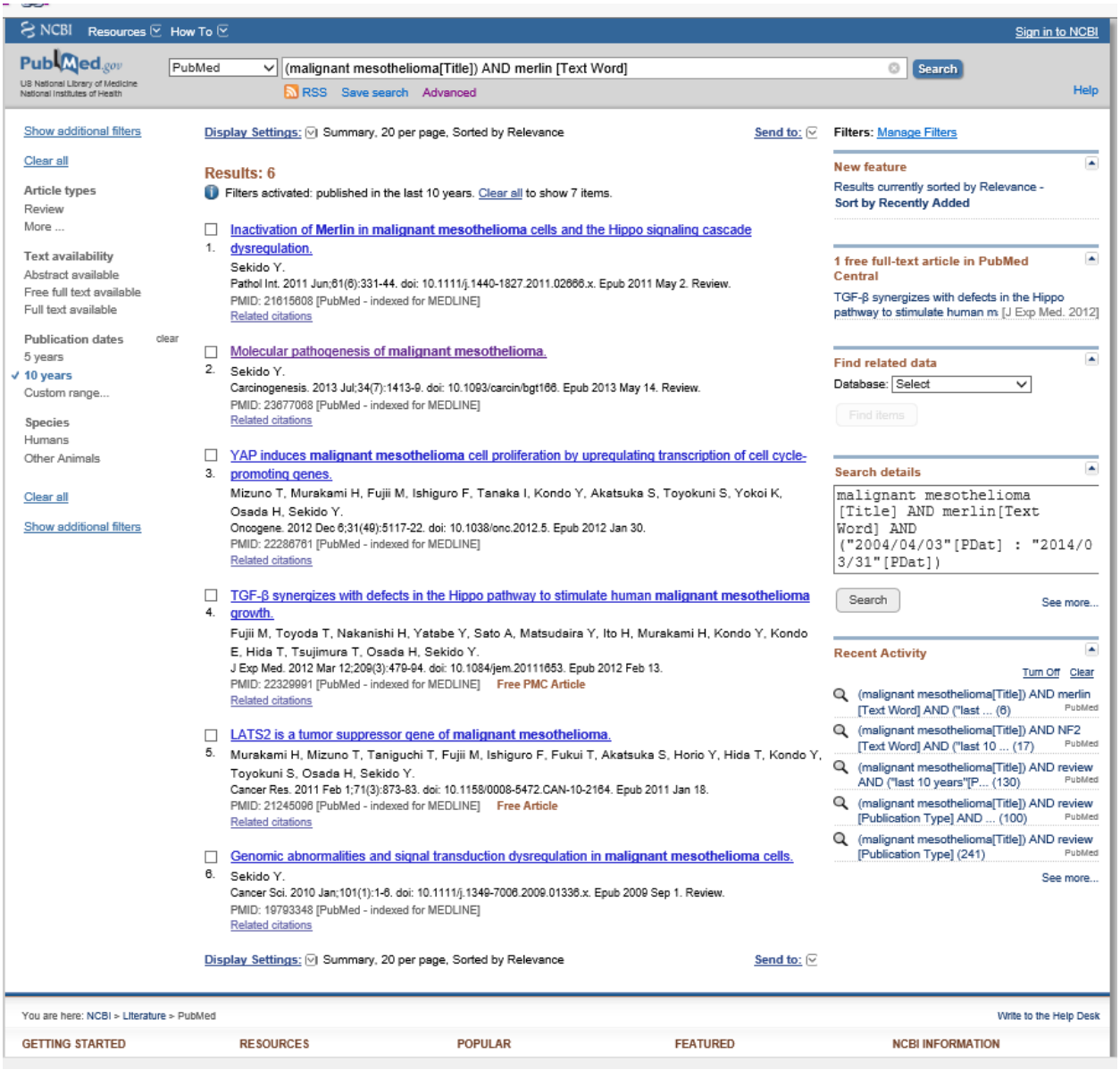
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